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Evaluating carnivore harvest as a tool for increasing elk calf survival and recruitment

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Project Background

Elk (*Cervus canadensis*) are an iconic species throughout the western United States and play a large role across ecological (Kauffman et al. 2010), social (Haggerty and Travis 2006) and economic (US Department of the Interior et al. 2014) landscapes. However, since the early 2000's, declines in elk numbers and recruitment (i.e., calf survival from birth to age 1) in some parts of the western United States resulted in concerns that the recovery of large carnivores such as wolves (*Canis lupus*), mountain lions (*Puma concolor*) and grizzly bears (*Ursus arctos*) has affected elk populations (Bunnell et al. 2002, Griffin et al. 2011a). Thus, wildlife managers are increasingly focused on understanding and managing the effects of predation on elk populations. Carnivore recovery is important to elk populations because predation may be a proximate limiting and regulating factor for many elk populations (Messier 1994, Hebblewhite et al. 2002, Garrott et al. 2008c). In addition to carnivore recovery, changing elk harvest management prescriptions, shifts in land use, and changing habitat and climatic conditions all contribute to a complex suite of variables with the potential to affect elk population dynamics. Because of this complexity, understanding the effects of predation on elk population dynamics is difficult, and determining appropriate management actions is challenging.

In the western United States, carnivore recovery has had varying effects on ungulate populations as the effects of carnivore predation on ungulates populations are complex and vary across systems with different carnivore-ungulate assemblages (Garrott et al. 2008)). In some areas, bear predation is an important mortality source for calves (Raithel 2005, Smith, et al. 2006, White et al. 2010, Lukacs et al. 2018), especially in areas where grizzly bear populations have increased over recent decades (Singer et al. 1997, Barber-Meyer et al. 2008). In other systems, mountain lion predation is the primary mortality source for calves (Myers et al. 1998, Johnson et al. 2013, Eacker et al. 2016). Although public attention is often focused on the effects of wolf recovery on ungulate populations, the effects of recovering wolf populations on ungulate populations has been shown to be variable (Hebblewhite et al. 2002, Vucetich and Peterson 2004, Barber-Meyer et al. 2008, Garrott et al. 2008b, White et al. 2010, Eacker et al. 2016b). Furthermore, if ungulate populations are limited by factors such as weather or habitat (Garrott et al. 2003, Griffin et al. 2011, Johnson et al. 2018) (...Johnson et al. 2019), or if predation is compensatory with other factors (Singer et al. 2003, Garrott et al. 2008), changes in carnivore populations may or may not result in changes in the key vital rates that drive ungulate population growth rate. These results highlight the importance of understanding the uncertainties associated with carnivore effects on ungulate populations as managers try to evaluate the efficacy of various management programs.

In situations where top-down effects (hunter harvest, predation, etc.) are believed to be limiting factors on ungulate populations, wildlife managers may turn to integrated carnivore-ungulate harvest management programs. These programs often employ a combination of liberalized carnivore and restrictive ungulate harvest regulations to achieve increases in the ungulate population. However, multiple factors affect the efficacy of integrated carnivore-ungulate management, including the duration of the carnivore control effort, the magnitude of the carnivore population reduction during treatment, weather conditions during and after the carnivore treatment (Boertje et al. 1996a), and interactions with other predators and prey in the system (Arthur and Prugh 2010, Prugh and Arthur 2015). In addition, multiple other sources of uncertainty affect the extent to which carnivore harvest regulations influence ungulate population

dynamics: First, objectives of the prescribed carnivore harvest regulation may or may not be achievable using hunter harvest (White et al. 2010, Bischof et al. 2012, N. Tatman et al. 2018). Second, realized carnivore harvest may or may not result in a biologically significant change in carnivore population abundance. Third, a change in carnivore abundance (even if harvest is achieved) and the associated predation rate may or may not affect ungulate population growth rate (Boertje et al. 2010, White and Garrott 2005, Melis et al. 2009). As such, the effectiveness of integrated carnivore-ungulate management programs may be difficult to assess and likely varies across ecological systems (Boertje et al. 1996, Hayes et al. 2003, White et al. 2010, Hurley et al. 2011, Keech et al. 2011, N. M. Tatman et al. 2018).

Evaluating the effects of integrated carnivore-ungulate management on carnivore and ungulate populations requires estimating important population parameters of both carnivore and ungulate populations before and after harvest prescriptions are implemented. As such, an initial step in evaluating the efficacy of integrated carnivore-ungulate management is determining if carnivore harvest prescriptions achieve desired carnivore harvest and population management goals. Estimating carnivore population size is challenging however because carnivores often occur at low densities, are wide ranging and difficult to detect, and often violate closure assumptions employed in traditional capture-recapture population estimation. However, recent advances in spatial capture recapture modeling provide improved methods of estimating carnivore population size (Proffitt et al. 2015, Boulanger et al. 2018, Paterson et al. 2019), allowing wildlife managers to monitor carnivore population abundances before and after implementing harvest prescriptions.

In addition to monitoring changes in carnivore abundances, managers need to evaluate ungulate population demography pre- and post- harvest treatment to determine if changes in carnivore populations result in changes in ungulate vital rates, and, ultimately, population growth rate and abundance. Survival of prime-aged females and recruitment can both have strong impacts on a population's trajectory (Gaillard et al. 1998, 2000, Eacker et al. 2016). However, while adult female survival is often high and relatively stable (Nelson and Peek 1982, Garrott et al. 2003), juvenile survival tends to be highly variable and consequently, may be a more common driver of ungulate population dynamics (Raithel et al. 2007, Harris et al. 2008). Therefore, recruitment, which incorporates fecundity and juvenile survival to age 1, represents an important demographic parameter that wildlife managers often use to track trends in population growth rates (DeCesare et al. 2012).

In west-central Montana, recovering carnivore populations concurrent with low recruitment and overall declines in ungulate populations raised public concerns about the effects of increasing carnivore populations on ungulate populations (Eacker et al. 2016). In this area, calf recruitment is a primary factor affecting elk population growth (Raithel et al. 2007, Eacker et al. 2017), and recent studies in this area have indicated mountain lion predation as the primary source of calf mortality (Eacker et al. 2016, Forzley et al. 2019). In response to these concerns, wildlife managers in Montana Fish, Wildlife and Parks (MFWP) Region 2 implemented an integrated carnivore-ungulate harvest management plan designed to increase elk populations through a reduction in carnivore abundance via increased hunter harvest in conjunction with more restrictive elk harvest management. A primary objective of the carnivore harvest management program was to reduce mountain lion populations by approximately 30% over three

watersheds within the region that had declining ungulate recruitment and populations, while maintaining stable mountain lion populations in a fourth watershed that was not experiencing declining ungulate recruitment and populations. The desired 30% reduction in populations was intended to temporarily reduce the mountain lion population, with a goal of reducing the mountain lion predation rate on elk while conserving the long-term viability of mountain lion populations in the area. Additionally, black bear (*Ursus americanus*) and wolf harvest regulations were liberalized during this period, in an effort to further reduce predation rates on elk and elk calves.

These recent changes in carnivore management in west-central Montana provide a unique opportunity to assess the efficacy of an integrated carnivore-ungulate management program by building on a recently completed project, and conducting a robust, multi-scale Before-After-Control-Impact evaluation of the effects of carnivore management on carnivore population density and elk calf survival and recruitment. During 2011-2014, we evaluated elk calf survival rates, and rates of predation from mountain lions and other large carnivores in the area (Eacker et al. 2016). We also estimated pre-treatment mountain lion density in an area managed for mountain lion reduction (Bitterroot study area) and an area managed for stability (Upper Clark Fork study area). Building from these previous efforts, the purpose of this project was to evaluate elk calf survival, cause-specific mortality, and population growth rates, as well as carnivore densities, to assess the effect of carnivore harvest management prescriptions on carnivore densities and elk populations.

Location

Elk calf survival and mountain lion population estimation is focused primarily within Ravalli County, Montana. Portions of this project also occur in Mineral, Missoula, Granite, Deer Lodge, and Powell Counties.

Study Objectives (2019-2020)

For the 2019-2020 period of this study, the primary objectives were:

1. Evaluate the extent to which lion harvest and density is controlled by wildlife management prescriptions (liberalized public harvest regulations).
2. Evaluate the extent to which wolf harvest and density is controlled by wildlife management prescriptions (liberalized public harvest regulations).
3. To estimate the relative effects of factors wildlife managers have some degree of control over in the short term (carnivore density), some degree of influence over in the long term (habitat-related nutritional differences), and factors wildlife managers cannot control (weather, landscape attributes) on elk calf recruitment in west-central Montana.
4. To evaluate the effects of carnivore harvest regulations on elk calf survival and cause specific mortality rates

Objective #1: Evaluate the extent to which lion harvest and density is controlled by wildlife management prescriptions (liberalized public harvest regulations).

To evaluate the effects of the mountain lion harvest management prescription on mountain lion population abundance, we compared mountain lion abundance in a treatment and control area before and after 4-years of increasing mountain lion harvest quotas in the treatment area. In February 2012, the Montana Fish and Wildlife Commission adopted a mountain lion harvest management structure for west-central Montana intended to reduce mountain lion abundance by 30% over across three watersheds in west-central Montana including the Bitterroot study area (treatment area) and manage lion population sizes for stability across one watershed that included the Upper Clark Fork study area (control area, Figure 1.1). During 2012 and 2013, we estimated pre-treatment mountain lion abundance in the treatment and control areas. We then measure post-treatment mountain lion abundance in the treatment and control areas in 2016 and 2017, respectively.

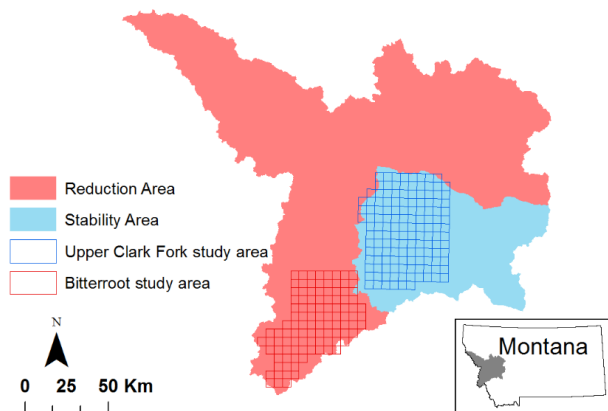


Figure 1.1 Mountain lion harvest management goals in west-central Montana during 2012-2015 were to reduce mountain lion abundance by 30% across a portion of the region (shaded red) and maintain stable abundances across a portion of the region (shaded blue). The Bitterroot study area (red grid) was located in an area managed for a 30% reduction in mountain lion abundance and the Upper Clark Fork study area (blue grid) was located in an area managed for maintaining stable mountain lion abundance.

Mountain lion harvest regulations and harvest

During the six years of this study (2012–2017), the prescribed harvest quotas for male and female mountain lions were mostly achieved, and management success (percent of the prescribed quota achieved) was high. In the Bitterroot treatment area, the average prescribed male and female quota was 3.4 males and 2.9 females per 1000km²/year, and the average harvest was 3.1 males and 2.6 females per 1000km²/year (Table 1.1). The average male and female harvest management success was 92% and 85%, respectively. In the Upper Clark Fork control area, the average prescribed male and female quota was 2.7 males and 0.8 females per 1000km²/year, and the average achieved harvest was 2.1 male and 0.5 females per 1000km²/year. The average male and female harvest management success was 79% and 70%, respectively (Table 1.1).

Table 1.1 *The male and female mountain lion harvest prescribed quotas and achieved harvest for the Bitterroot and the Clark Fork study areas in west-central Montana during 2012–2017. The Bitterroot study area included lion management units 250 and 270 and was managed for mountain lion population reduction (treatment area), and the Clark Fork study area included lion management units 211/216, 210, 212/215, and 213/214 and was managed for stable mountain lion population abundance (control area). The female harvest quota (number per 1000 km²) is reported for comparison because the area of the Bitterroot and Clark Fork study areas differed.*

Prescription Type	Study area	Year	Male quota	Male harvest	Female quota	Female harvest	Female quota per 1000 km ²	Female harvest per 1000 km ²
Treatment	Bitterroot	2012	14	12	14	15	4.20	4.50
Treatment	Bitterroot	2013	8	10	12	11	3.60	3.30
Treatment	Bitterroot	2014	10	8	7	6	2.10	1.80
Treatment	Bitterroot	2015	11	11	8	4	2.40	1.20
Treatment	Bitterroot	2016	11	7	8	8	2.40	2.40
Treatment	Bitterroot	2017	11	13	8	7	2.40	2.10
Control	Clark Fork	2012	20	13	3	3	0.44	0.44
Control	Clark Fork	2013	16	16	4	4	0.58	0.58
Control	Clark Fork	2014	16	13	6	6	0.87	0.87
Control	Clark Fork	2015	16	16	5	3	0.73	0.44
Control	Clark Fork	2016	16	10	5	4	0.73	0.58
Control	Clark Fork	2017	16	13	5	1	0.73	0.15

Mountain lion population abundance

We used a spatially unstructured sampling design coupled to a spatially explicit capture-recapture (SCR) model to estimate mountain lion abundance in the treatment and control areas, pre- and post-harvest treatment. Our approach used direct search effort by hound handlers and trackers in the study area to collect scat, hair and muscle samples for genetic analysis, allowing

for individual mountain lion identification. The spatial locations of these samples were then used in a hierarchical model to estimate the relationship between mountain lion density and the underlying value of the statewide mountain lion resource selection function (Robinson et al. 2015). Additionally, we used spatial information from collared mountain lions to further inform sex-specific patterns of space use in the SCR model. This approach that integrated space use information from both recaptures and collars simultaneously reduced the bias and improves the precision of the resulting mountain lion abundance estimates.

The number of sampling-days, amount of search effort, number of samples included in analysis, the number of individuals identified, and the number of spatial recaptures varied across the two study areas and two time periods (Table 1.2). The number of individuals identified and the number of spatial captures in each study area and time period, together with previous simulation-based work on the same study design, suggest that each dataset is adequate to result in unbiased spatial-capture recapture abundance estimates (Table 1.2, Paterson et al. 2019).

Table 1.2 *The number of sampling-days, search effort (in km), number of male and female samples included in analyses, and the number of individual male and female mountain lions detected in the Bitterroot and Clark Fork study areas in west-central Montana during 2012–2017.*

Study area	Year	Number sampling- days	Search effort (km)	Number of samples		Number of individuals detected	
				Female	Male	Female	Male
Bitterroot	2012	50	8897	50	28	37	25
Bitterroot	2016	84	14,216	41	33	33	21
Clark Fork	2013	66	12,898	37	23	21	14
Clark Fork	2017	95	10,905	39	27	25	17

To estimate pre- and post-treatment abundance of mountain lions in the treatment and control areas we pooled information collected throughout this project and developed a multi-strata spatial-capture model. The multi-strata SCR model incorporated spatial capture-recapture data from the Bitterroot and Clark Fork study areas across all years and used information from collared individuals to help inform how animals used space. We used the estimated relationship between the mountain lion resource selection function (RSF) and the abundance of activity centers combined with estimated sex ratios to extract the predicted abundances for each study area during pre- and post-harvest treatment periods (Table 1.3). In the Bitterroot study area we found an overall decline in abundance, along with a change in the sex ratio from 2012 (M:F = 0.50 [0.33, 0.67]) to 2016 (M:F = 0.28 [0.17, 0.40]; Table 1.3). This translated into a decline in the abundance of males, and similar abundances of females. In the Upper Clark Fork study area, we found evidence for an increase in overall abundance but no meaningful change in the sex ratio between 2013 (M:F = 0.42 [0.26, 0.58]) and 2017 (0.39 [0.25, 0.54]), resulting in similar abundances of male and female animals between the two time periods (Table 1.3).

Table 1.3 Predicted male and female mountain lion abundance (*N*), density (animals per 100km²), and 90% credible intervals (LCI, UCI) of total, male, and female mountain lions within in the Bitterroot and Clark Fork study areas (i.e. trapping grids) during 2012–2017.

Study Area	Year	Group	N	90%LCI	90%UCI	Density	90%LCI	90%UCI
Bitterroot	2012	Total	161	104	233	6.13	3.96	8.88
Bitterroot	2012	Males	80	52	116	3.05	1.98	4.42
Bitterroot	2012	Females	81	52	117	3.09	1.98	4.46
Bitterroot	2016	Total	115	69	173	4.38	2.63	6.59
Bitterroot	2016	Males	33	20	49	1.26	0.76	1.87
Bitterroot	2016	Females	82	49	124	3.12	1.87	4.72
Clark Fork	2013	Total	57	37	85	1.68	1.09	2.5
Clark Fork	2013	Males	24	16	36	0.71	0.47	1.06
Clark Fork	2013	Females	33	21	49	0.97	0.62	1.44
Clark Fork	2017	Total	72	47	105	2.12	1.38	3.09
Clark Fork	2017	Males	28	18	41	0.82	0.53	1.21
Clark Fork	2017	Females	44	29	64	1.3	0.85	1.88

Objective #2: Evaluate the extent to which wolf harvest and density is controlled by wildlife management prescriptions (liberalized public harvest regulations).

Wolves recolonized the Bitterroot Valley in the early 2000’s leading to concern regarding the potential effects of wolves on elk abundance and recruitment. Prior to 2011, wolves in the Bitterroot Valley were part of the experimental non-essential population that resulted from the reintroduction of wolves into the Central Idaho Experimental Area in 1995-96. In May 2011, wolves in Montana became subject to state management authority guided by the Montana Wolf Conservation and Management Plan. Across Montana, minimum wolf counts increased steadily until 2011. Since 2011, the statewide minimum counts and population estimates have been stable to declining, which is at least partially due to decreased effort to identify all wolves, and local population abundance varies annually with harvest management goals, management of livestock-wolf conflict, and other biological factors (Coltrane et al. 2016). Beginning in 2011, as part of the west-central Montana management to reduce carnivore densities, wolf harvest management prescriptions were implemented in the Bitterroot study area to reduce wolf population densities. Our objectives are to evaluate the effects of wolf harvest management regulations on realized wolf harvest and population abundance in the south Bitterroot study area.

Wolf harvest regulations and harvest

Between 2008 and 2011, wolves in Montana were federally delisted, relisted, and then delisted again (Hanuska-Brown et al. 2011). This process resulted in a Montana wolf hunting season in 2009, no hunting season in 2010, and hunting seasons from 2011 through the present. Since 2011, wolves in Montana have been subject to state management authority guided by the Montana Wolf Conservation and Management Plan. As part of management objectives to reduce carnivore densities in west-central Montana, wolf harvest management prescriptions were implemented in the Bitterroot Valley study area to reduce wolf population densities. Since 2011, there are no wolf harvest limits specific to the West Fork or East Fork areas. Instead, harvest regulations are based on combined hunting and trapping bag limits of wolves per person. In 2012, wolf harvest regulations limited each person to harvesting a maximum of 3 wolves. From 2013 until present, wolf harvest regulations limited each person to harvesting a maximum of 5 wolves.

Hunters and trappers are required to report all harvested wolves to MFWP, and we used these harvest data from 2008–2017 to track the number and location of wolves harvested annually. Since 2009, combined harvest (hunting + trapping) has ranged from 0-8 wolves per year in HD 250, and from 2-15 wolves per year in HD 270 (Table 2.1).

Wolf population estimation

MFWP uses a combination of radio-collaring efforts, direct observational counts, remote cameras, and track surveys to annually track the wolf population, to document pack size and breeding pair status of known packs, and to determine pack territories in our study area. Ground and aerial tracking occurs 1-2 times per month to locate VHF and GPS collared animals and count the number of wolves travelling together. Additional information on sightings, breeding activity, mortalities, and human-wolf conflicts is collected throughout the year. This information is used to estimate the minimum count of wolves per hunting district on December 31st of each year (Coltrane et al. 2016). In 2000, MFWP counted a minimum of 7 wolves in the entire Bitterroot Valley, and the minimum count increased to a high of 74 in 2011. In 2011, there was a minimum of 28 wolves in the West Fork (1.95wolves/100km²) and 8 wolves in the East Fork (0.47 wolves/100km²) of the south Bitterroot study area (Table 2.1).

Table 2.1 *The estimated minimum count of wolves in the HD 270 and HD 250 area of the south Bitterroot study area during 2001-2017.*

Year	HD 270 Minimum count	HD 270 Minimum number per 100 km ²	HD 270 Harvest	HD 250 Minimum count	HD 250 Minimum number per 100 km ²	HD 250 Harvest
2001	2	0.13	NA	5	0.27	NA
2002	5	0.33	NA	5	0.27	NA
2003	Not available	Not available	NA	4	0.22	NA

2004	Not available	Not available	NA	6	0.33	NA
2005	Not available	Not available	NA	11	0.60	NA
2006	10	0.66	NA	11	0.60	NA
2007	17	1.13	NA	14	0.77	NA
2008	15	1.00	NA	19	1.04	NA
2009	13	0.86	3	24	1.31	4
2010	20	1.33	NA	30	1.64	NA
2011	8	0.53	3	28	1.53	6
2012	10	0.66	4	23	1.26	8
2013	12	0.80	4	16	0.87	3
2014 ¹	21	1.22	2	12	0.84	1
2015	15	0.87	2	11	0.77	2
2016	15	0.87	15	14	0.97	2
2017	19	1.11	10	14	0.97	0

¹ *There was a boundary change that expanded HD 270 and reduced the size of HD 250.*

Objective #3: To estimate the relative effects of factors wildlife managers have some degree of control over in the short term (carnivore density), some degree of influence over in the long term (habitat-related nutritional differences), and factors wildlife managers cannot control (weather, landscape attributes) on elk calf recruitment in west-central Montana.

The trajectories of ungulate populations through time are the integrated result of a group of co-varying vital rates (e.g., survival, reproduction, recruitment), and effective population management requires the identification of those rates responsible for demographic performance (Johnson et al. 2010). Although variation in adult female survival rates has the highest proportional impact on population growth rate, theoretical and empirical work strongly suggest that adult survival rates are buffered against high variation (Pfister 1998, Gaillard and Yoccoz 2003, Jäkäläniemi et al. 2013, Péron et al. 2016). In contrast, juvenile survival has a lower proportional impact on growth rate but much higher temporal variation, such that it can have a large impact on population growth rates (Gaillard et al. 1998, Raithel et al. 2007, Eacker et al. 2017). Thus, juvenile survival is commonly monitored and used as an index of population performance. However, juvenile survival varies annually, and causes of mortality differ widely across ecosystems (Raithel et al. 2007, White et al. 2010), which makes it difficult to understand and make generalizations about sources of variation in juvenile survival.

Here, our goal was to analyze a time-series of data on harvested elk populations in west-central Montana that contained spring count and fall harvest data to investigate and identify important sources of variation in recruitment. We used a population modeling approach to evaluate the per capita elk calf recruitment rate, and factors affecting elk calf recruitment rates. Importantly, this modeling approach uses data that are already routinely collected by wildlife

managers, i.e., the numbers of individuals observed in each class, to make inference about the key vital rate for which age-ratios are a proxy: the per capita recruitment rate that can drive the population dynamics of ungulates.

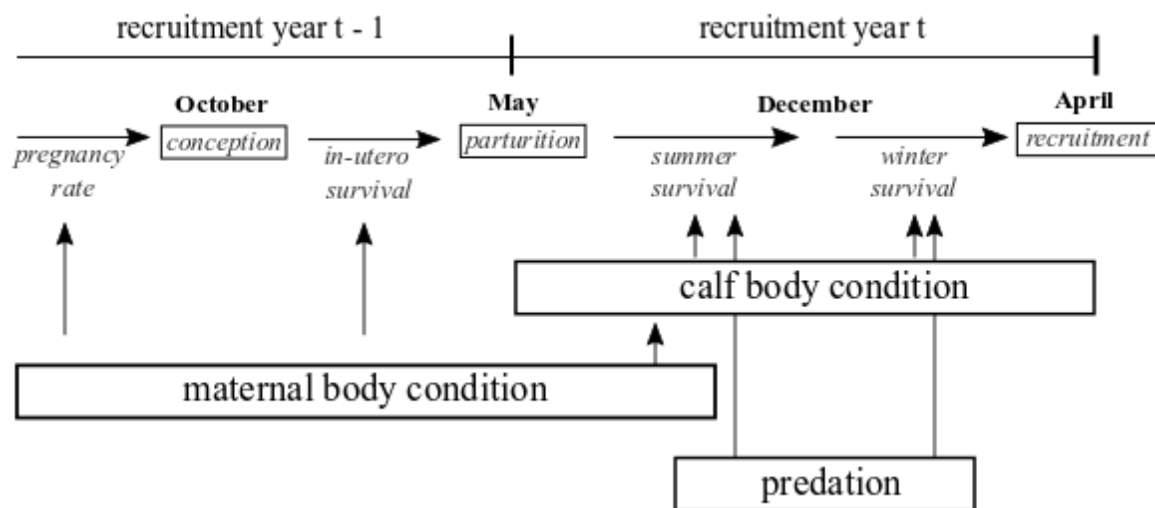


Figure 3.1 Concept diagram illustrating the progression of events and rates underlying recruitment for spring surveys. The probability that each calf is available to be surveyed during the late spring surveys is the product of pregnancy rates, in-utero survival to parturition, then summer and winter survival, the product of which is the per capita recruitment rate. Each rate is hypothesized to be associated with multiple drivers related to the timing of events.

The per capita recruitment rate is the result of a series of processes that are potentially affected by environmental conditions and predator pressure (Figure 3.1). Maternal body condition from the summer prior to conception through parturition has been shown to be related to pregnancy rates (Bonenfant et al. 2002, Cook et al. 2004), calf parturition mass (Bender et al. 2002) and neonatal survival during the maternal care period following birth (Griffin et al. 2011). Therefore, we expected per capita recruitment rates to be positively associated with indices of nutrition (year $t-1$), negatively associated with winter severity (year $t-1$), and potentially demonstrate an interaction between nutrition indices and winter severity such that poor summer conditions and severe winter conditions combine to further reduce recruitment (Cook et al. 1996). Environmental conditions experienced after parturition (year t) are thought to be related to juvenile survival in its first year, either through direct impact on juvenile nutrition through foraging (Cook et al. 1996) or as mediated through maternal provisioning during the maternal care period (Cook et al. 2004). There is an evolving debate as to whether spring conditions or late summer conditions are more important to juvenile survival (Hurley et al. 2014), and we split indices of the nutritional environment into spring and summer periods to assess the relative importance of these two periods. We expected per capita recruitment rates to be positively associated with indices of nutrition (year t). Juvenile survival to recruitment has been shown to be related to winter conditions (Loison and Langvatn 1998) and we expected per capita recruitment rates to be negatively associated with winter severity (year t), and interact with nutritional conditions such that the impact of poor nutritional conditions is made worse in severe winters. Predators can have a large impact on juvenile survival (Barber-Meyer et al. 2008,

White et al. 2010, Brodie et al. 2013, Eacker et al. 2016), and we expected per capita recruitment rates to be negatively associated with indices of predator abundance.

Methods

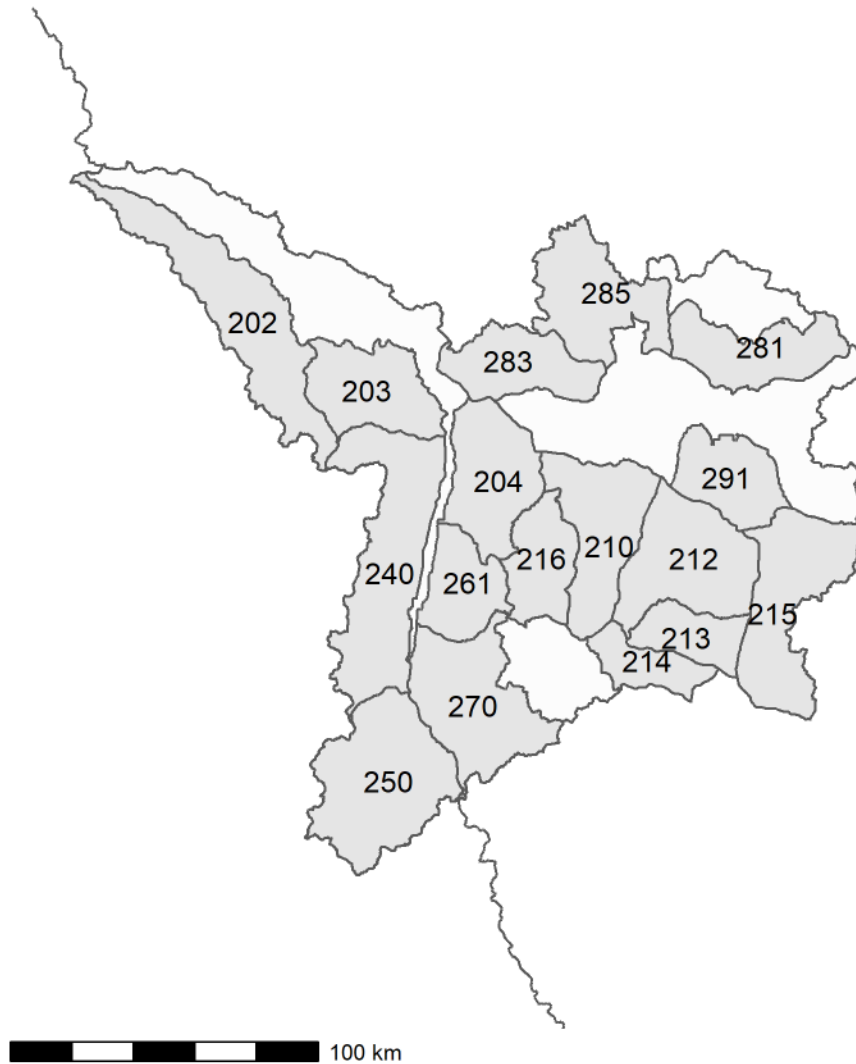


Figure 3.2 The elk hunting districts in west-central Montana used for analysis. We restricted our analysis to those hunting districts with at least 6 years of data.

Elk count and harvest data

For our analyses of elk recruitment, we used data from seventeen hunting districts in west-central Montana (Figure 3.2). These HDs included, but were not limited to, the Bitterroot and Upper Clark Fork study areas. We used annual spring elk count and age/sex classification data collected from fixed wing aircraft. Surveys were conducted annually on the winter range for each district in the late spring prior to the migration to summer range and the birth pulse. Due to logistical limitations, not every district had count and age/sex classification data for each of the

13 years (2004 to 2016), which generated a discontinuous time series for most districts (median number of years = 7, minimum = 6, maximum = 13). In our analysis, we included all hunting districts that had a minimum of 6 years of count data collected during 2004 to 2016. For a small number of district-years a total count was available, but no age/sex classification was reported ($n = 5$). For the population modeling approach, we were able to treat the age/sex classifications in these years as missing data. Moreover, in each district-year not all of the animals that were counted were subsequently classified according to age/sex class, i.e., the number of animals that were classified into each age and sex category represented a sample of the total number of animals that were counted. Moreover, throughout this period there were instances where animals were counted but not classified, resulting in total counts but no classification information?

We aggregated data on the fall elk harvest (calves, adult females and adult males) as estimated by the state wildlife agency. For the population model (see below), we included the estimated number of calves, adult females and adult males harvested.

Population model description

The population model approach linked two separate processes: 1) a model for the biological processes of elk survival, recruitment and harvest, and 2) the observation process that gave rise to data. We defined the annual population cycle from the birth pulse (in May-June) to the following spring (March-April) when calves recruit to the population as 1-year-olds. The population cycle can be represented as an age-structured matrix model, where the expected number (E) of calves (N_c), adult females (N_{af}) and adult males ($N_{adult,m}$) in year t and district u is given as:

$$E \begin{Bmatrix} N_{t,u}^c \\ N_{t,u}^{af} \\ N_{t,u}^{am} \end{Bmatrix} = \begin{Bmatrix} \tau N_{t-1,u}^{af} - h_{t,u}^c \\ \phi_a (\delta N_{t-1,u}^c + N_{t-1,u}^{af} - h_{t,u}^{af}) \\ \phi_a ((1 - \delta) N_{t-1,u}^c + N_{t-1,u}^{am} - h_{t,u}^{am}) \end{Bmatrix}$$

where the vital rates that connect the population size across years are apparent adult survival (ϕ_a), the proportion of calves that were female (δ , here assumed to be equal to 0.5), and the per capita recruitment rate (τ), and h^c , h^{af} , and h^{am} are age/sex specific harvest. Here we assumed the survival of all age/sex classes other than calves was the same through time. Per capita recruitment is the product of a series of vital rates, including the probability of conception, in-utero survival to birth, and then calf survival from birth to census the next spring. Additional modeling details are described in Paterson et al. (2019b).

Covariates

Our primary goal was to assess the strength of evidence for a series of potential sources of variation in the recruitment of elk calves as mediated through maternal body condition, calf body condition and predation risk (Figure 3.1). We developed covariates to index environmental conditions during the summer growing season, winter severity, and predator abundances. We estimated the average cumulative precipitation values within each elk population range over the

spring (neonatal period, May - June) and the summer periods (juvenile independence period, July – September, PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, accessed 11 September 2018). As an index of summer growing season conditions, we estimated the average annual integrated-NDVI values within each elk population range over the spring and summer periods. As an index of winter severity, we used snow-water equivalent (swe), a metric of snowpack density. We estimated the mean cumulative swe for each population range from December 1 to April 31 of each year.

Information on carnivores was available from harvest records (mountain lion and black bears) and annual surveys (wolves). State regulations require that all harvested mountain lions and black bears that are harvested be presented with intact evidence of sex to FWP staff, and these harvest data were available through all years and for all districts in our study. End-of-the-year minimum wolf counts (number observed by December 31 of each year) were available as part of the state of Montana’s wolf monitoring program and management plan. We used the number of harvested mountain lions and black bears and wolf counts as covariates in the models, hypothesizing that they were an index to the underlying populations.

Results

The number of elk counted, observed age ratios, and harvested elk varied considerably among years and hunting districts (Figure 3.3). Antlerless and antlered harvest varied across years and hunting districts in response to changing regulations over the time period of the study. Notably, high harvest in some districts from 2004 to 2007 was followed by reduced harvest.

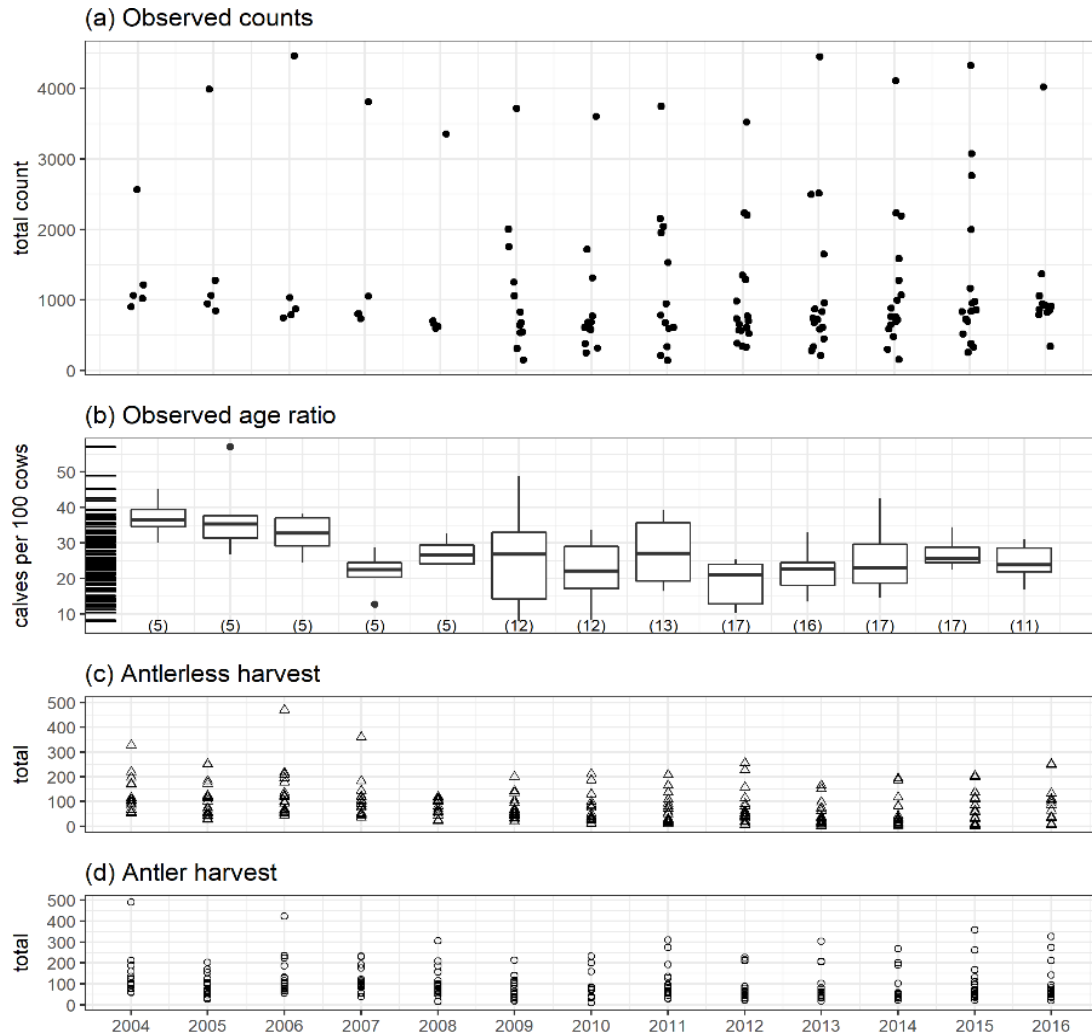


Figure 3.3 Summary of observed elk count and classification data and estimated antlerless and antlered harvest for the 17 hunting districts included in the elk population model. Both observed counts and age ratios (sample size in parentheses) demonstrated large variation among years and hunting districts. Similarly, antler and antlerless harvest varied through time and district. In panel (a), the observations have been jittered along the x-axis to improve visibility. In panel (b), the y-axis includes a rug that highlights the distribution of the data.

Sources of variation in recruitment

We found strong evidence for a series of relationships between covariates and recruitment using the population model. For an average year and with all covariates held to their average value (zero for standardized covariates), our model predicted an overall mean recruitment rate of 0.25 (90% CI = [0.21, 0.29]). For each covariate below, we report the estimated effect on the logit scale and then a prediction of how recruitment changed from this overall mean as that covariate increased/decreased one standard deviation from the average value. We found a weak negative association between mountain lion harvest and per capita recruitment rates ($\hat{\beta}_{lions} = -0.04$ [-0.07, 0]), which corresponded to a decline in per capita recruitment from the overall mean of 0.25 (90% CI = [0.21, 0.29]) at the average lion harvest

(4.12 harvested) to 0.24 [0.19, 0.27] at one standard deviation above the average lion harvest (7.88 harvested). Similarly, we found a weak association between black bear harvest and per capita recruitment rates ($\hat{\beta}_{bears} = -0.05$ [-0.09, 0]), declining from the overall mean (0.25 [0.21, 0.29]) at the average black bear harvest (21.31 harvested) to 0.24 [0.21, 0.28] at one standard deviation above the average black bear harvest (39.17 harvested). However, we found strong evidence for an interaction with cumulative snow water equivalent (swe) ($\hat{\beta}_{bears*swe} = -0.11$ [-0.16, -0.05]) that became different from zero only at higher bear harvests and more severe winters. At the average black bear harvest, per capita recruitment rates in a mild winter (hereafter defined as the 5th percentile of standardized swe values, swe = -0.95), average winter (swe = 0), or severe winter (hereafter defined by the 95th percentile of swe values, swe = 2.22) showed no meaningful difference. At one standard deviation above the average black bear harvest recruitment in a mild winter was higher than in a mean winter (difference = 0.02 [0.01, 0.04]), and even higher than in a severe winter (difference = 0.07 [0.03, 0.12]). In contrast, we found a weak positive association between wolf counts and recruitment ($\hat{\beta}_{wolves} = 0.05$ [0, 0.09]), increasing from the overall mean (0.25 [0.21, 0.29]) at the average wolf count (15.99 wolves) to 0.26 [0.22, 0.30] at one standard deviation above the average wolf count (30.49 wolves). However, we also found strong evidence for a negative interaction with cumulative snow water equivalent ($\hat{\beta}_{wolves*swe} = -0.06$ [-0.11, -0.02]) such that recruitment declined with high wolf counts and increasing winter severity. At one standard deviation above the average wolf count recruitment in a mild winter was higher than in a mean winter (difference = 0.02 [0.01, 0.03]), and even higher than in a severe winter (difference = 0.06 [0.03, 0.09]).

We also found strong evidence for an association between several environmental covariates that corresponded to conditions when the calf is on the ground and per capita recruitment. Cumulative spring precipitation had a negative association with per capita recruitment rates ($\hat{\beta}_{springPrecip} = -0.2$ [-0.26, -0.14]), declining from the overall mean at the average spring precipitation (0.17 m) to 0.21 [0.18, 0.25] at one standard deviation above the average spring precipitation (0.22 m). In comparison, cumulative summer precipitation had a weaker positive association with recruitment ($\hat{\beta}_{summerPrecip} = 0.08$ [0.03, 0.13]), increasing from the overall mean at the average summer precipitation (0.15 m) to 0.27 [0.23, 0.31] at one standard deviation above the average summer precipitation (0.19 m), and strong evidence for an interaction with winter severity ($\hat{\beta}_{summerPrecip*swe} = 0.04$ [0, 0.07]) such that low values of summer precipitation combined with winter severity to reduce per capita recruitment. At one standard deviation below the average summer precipitation (0.11 m), recruitment was higher in a mild winter than in an average one (difference = 0.02, [0.01, 0.03]), and even higher than in a severe winter (difference = 0.04, [0.01, 0.07]). Although we found no evidence for a main effect of spring NDVI, we found evidence for an interaction with winter severity ($\hat{\beta}_{springNDVI*swe} = 0.05$ [0.01, 0.1]). Low values of spring NDVI combined with severe winters were associated with reduced recruitment. At one standard deviation below the average spring NDVI (0.81), recruitment was again higher in a mild winter than an average winter (difference = 0.02 [0, 0.03]) and a severe winter (difference = 0.05 [0.01, 0.08]).

Finally, we also found strong evidence for an association between environmental variation during the year in which the calf is in-utero and recruitment. We found strong evidence for a negative association with lagged winter severity ($\hat{\beta}_{swe[t-1]} = -0.06$ [-0.1, -0.01] (0.25, [0.21, 0.29] at the average swe (8.15 m) to 0.23 [0.20, 0.28] at one standard deviation above the average swe (14.45 m). Although we did not find evidence for a main effect of summer NDVI,

we found strong evidence for an interaction with winter severity ($\hat{\beta}_{summerNDVI*swe[t-1]} = 0.08$ [0.05, 0.12] such that recruitment at low summer NDVI (1 standard deviation below the mean) was higher in a mild winter than a mean winter (difference = 0.03 [0.02, 0.04]), and considerably higher than in a severe winter (difference = 0.08 [0.05, 0.12]).

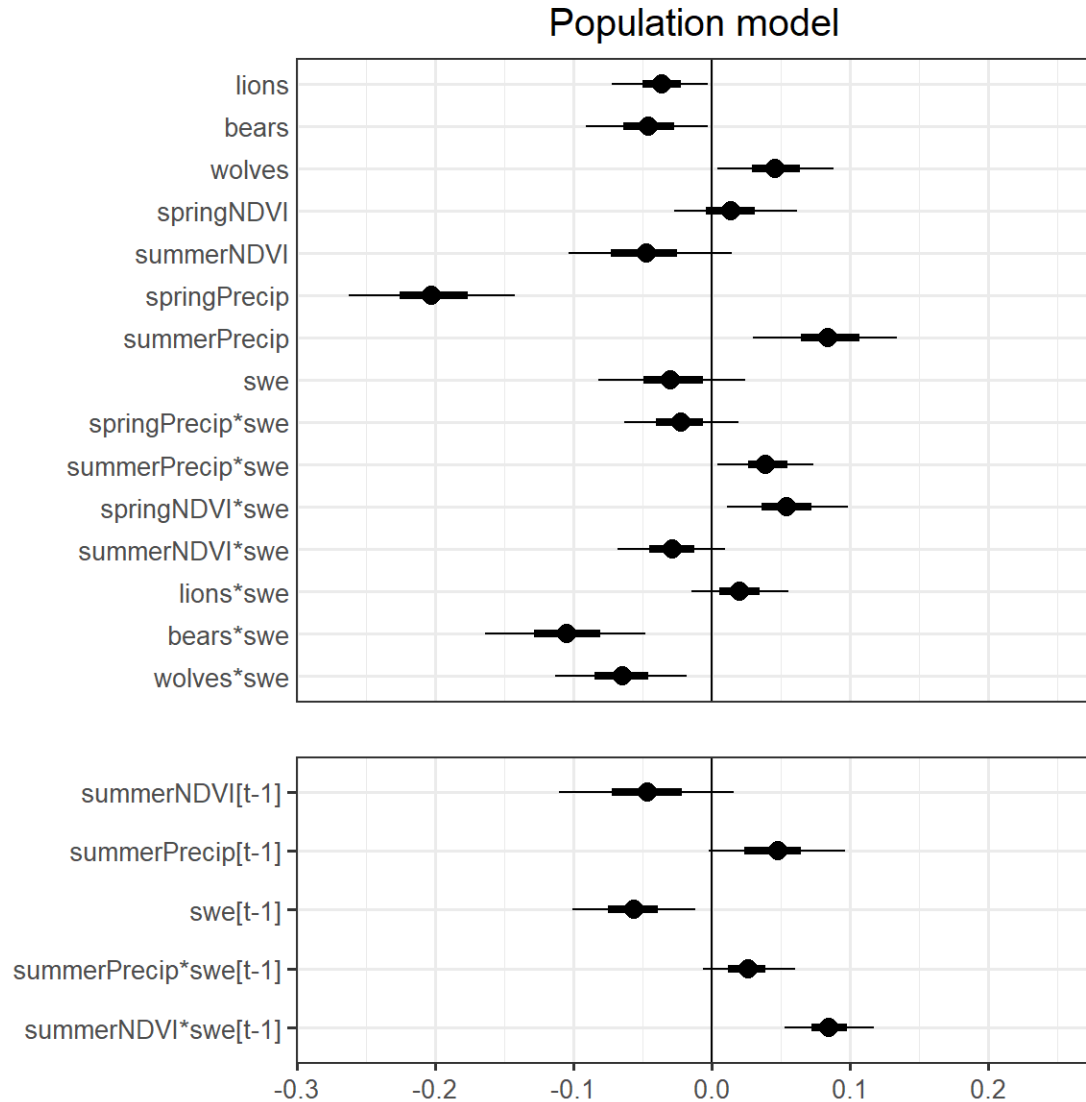


Figure 3.4 Estimated regression coefficients for standardized covariates. The black dot denotes the median of the approximate posterior distribution, the heavy black line the 50% highest posterior density interval (HPD) and the light black line the 90% HPD interval.

Discussion

We found that environmental conditions experienced by the calf on the ground (year t , related to calf survival) and the female prior to conception and when the calf is in-utero (year $t-1$)

were strongly connected to per capita recruitment rates. Contrary to our expectations, cumulative spring precipitation in year t was negatively associated with recruitment. A post-hoc analysis of the precipitation signal strongly suggested that these high values of spring precipitation were the result of heavy snow on the summer range, an observation consistent with previous work on elk in this larger system (Lukacs et al. 2018). Cold and wet springs are thought to be a risk factor for elevated neonatal mortality, as environmental conditions interact to predispose neonates to the effects of illness, delayed green-up and increase risk of predation (Adams et al. 1995, Tveraa et al. 2003). Summer precipitation during year t and year $t-1$ was strongly, positively associated with recruitment. We also found evidence to support an interaction between summer precipitation values and winter severity in year t such that dry summers interacted with particularly severe winters to diminish calf survival in year t . Precipitation is known to be directly related to the rate of forage senescence, digestible energy and relative protein content (Onillon et al. 1995, MacKlon et al. 1996, Yang et al. 2001), thought to be key factors in determining the body condition of ungulates headed into winter (Link and Nichols 1994, Blanchard et al. 2003, Tollefson et al. 2011). Our results are broadly consistent with previous work concluding that body condition during this critical period is a key factor associated with overwinter survival in the case of calves on the ground, and with offspring survival the following spring in the case of pregnant females (J. G. Cook et al. 2004). In contrast to previous work that found the relationship between precipitation and recruitment to be relatively minor (Lukacs et al. 2018), we found spring and summer precipitation in year t to be major contributors to variation in recruitment. We also attribute the difference to our separation of precipitation into the two critical phases of spring (an index of early growing/environmental conditions) and summer (as an index of forage quality headed into winter). The use of a season-long precipitation metric could confound variation in these two periods such that only the most extreme combination (e.g., a very wet spring coupled to a dry summer) would be associated with variation in recruitment.

We found mixed evidence for a relationship between primary production (NDVI) and per capita recruitment rates. Although we found no evidence for a direct relationship between NDVI in either in the spring or summer during the year the calf is on the ground and recruitment, we did find evidence for an interaction between spring NDVI and winter severity such that years with combined low spring NDVI and severe winters were associated with diminished recruitment. Moreover, we found an interaction between summer NDVI and winter severity during the year the calf is in-utero (year $t-1$) that suggested that high values of summer NDVI and severe winters reduced recruitment. NDVI is frequently interpreted as an index of forage quality (Pettorelli et al. 2011), though the link between the two is uncertain and can depend on the NDVI metric used (Fryxell 1991, Hebblewhite et al. 2008, Johnson et al. 2018). Spring green-up as indexed by increasing NDVI values has been positively associated with body condition (Hamel et al. 2009), as the greening vegetation has high digestible energy and protein content, and the relative value of this phase of forage quality has been suggested as a driver of spring migrations (Merkle et al. 2016). We used a time-integrated NDVI metric where low values likely corresponded to a delayed start of seasonal plant growth and found the NDVI metric only become meaningful when followed by a severe winter, consistent with other work highlighting the interactive effects of nutrition and winter severity (Singer et al. 1997, Garrott et al. 2003), and broadly suggesting that calves can otherwise make up for a poor start in mild winter conditions. We also found strong evidence that summer NDVI and winter severity in year $t-1$ were related to recruitment through an interaction such that high values of summer NDVI in a severe winter were negatively associated with recruitment. This is not the first study to document

a surprising relationship between NDVI and the demographic performance of ungulates (Lukas et al. 2018), which highlights the care that must be taken in assuming NDVI represents the same thing across a growing season. The relationship between NDVI and forage quality may be fundamentally different in late summer, when the high primary production NDVI represents actually corresponds to diminished digestible energy (Hebblewhite et al. 2008). Alternatively, we speculate that summer NDVI values might be correlated to large scale, long-term weather patterns such that they are serving as a proxy for environmental conditions in the approaching winter. Further work is required to detail the link between NDVI and forage quality as it relates to ungulate nutrition and body condition, and we caution against the assumption that NDVI is a proxy for it.

Predation has been shown to be a major factor influencing juvenile elk survival in individual-based studies that allow for the estimation of cause-specific mortality (Barber-Meyer et al. 2008, Eacker et al. 2016). It is considerably more challenging to assess the effects of predators on vital rates when working at the population level, given accurate predator population estimates are difficult to attain and the effects of predation can be complicated by interacting effects with weather and resource limitation. In particular, studies need to be carefully designed when trying to assess how the harvest of predators is related to variation in the vital rates of prey (Boutin 1992). The connection between predator harvest, predator population dynamics and predation risk to ungulates is unclear and has rarely been evaluated (Wolfe et al. 2016). This lack of clarity is worsened where predator harvest regulations are set in response to a combination of social, biological, and political factors (Clark et al. 1996, Bruskotter 2013, Young et al. 2015). Although high harvest with heavy hunting pressure has been implicated in the declines of predator populations (Kolenosky 1986, Allen et al. 2018a), harvest numbers have also been positively associated with population sizes of predators (Clark et al. 1996, Bruskotter 2013, Young et al. 2015, Wolfe et al. 2016, Allen et al. 2018). Our results for the association between mountain lion and black bear harvest generally support this latter interpretation, as we found that the magnitude of harvest was negatively associated with per capita recruitment rates. For black bears, predation is thought to occur primarily during the neonate phase in late spring/early summer (Forzley 2019), and high harvest the following fall and spring may serve as a reasonable proxy for the population size of black bears during the birth pulse. On the other hand, we found a weak positive association between minimum wolf counts, ostensibly a more direct index of population size, and recruitment that we interpret as a spatial arrangement of predators on the landscape to take advantage of more productive areas (Fuller and Sievert 2001). That signal was swamped, however, by the interaction between wolf counts and winter severity that suggested high wolf counts interacted with severe winters to reduce recruitment. This result is consistent with prior work in the region (Brodie et al. 2013) (but see [Garrott et al. 2008a]), and we speculate that it may reflect an additive effect of predation to nutritional and environmental stress during severe winters. We stress that more work is needed to understand the relationship between minimum wolf counts, wolf abundance and vital rates. More generally, we echo the caution that adequately understanding the connections between predator indices (harvest or counts), predator population dynamics and ungulate vital rates requires carefully designed experiments (Boutin 1992).

This work has been published and the citation is:

Paterson, J. Terrill, Kelly Proffitt, Jay Rotella, and Robert Garrott. "An improved understanding of ungulate population dynamics using count data: Insights from western Montana." *PloS one* 14, no. 12 (2019).

Objective #4: To evaluate the effects of carnivore harvest regulations on elk calf survival and cause specific mortality rates

Our object in this portion of the study was to evaluate if elk calf survival rates, or rates of predation from mountain lions and other large carnivores in the area, differed before, during, or after the liberalized carnivore harvest management prescriptions. Our second objective was to understand the environmental factors and individual characteristics related to elk calf survival in the Bitterroot study area.

Methods

We compared elk calf survival and cause-specific mortality in the Bitterroot study area before, during, and after the mountain lion harvest treatment. The mountain lion harvest treatment was implemented in December of 2012 and lasted for two years, after which mountain lion harvest quotas were reduced. Therefore, we considered calves radio-tagged in the spring and fall of 2011 and monitored 2011–2012 as having occurred in the pre-treatment era. We considered calves tagged the spring and fall of 2012 as having occurred during the pre-treatment era for their first summer and the during-treatment era for their first winter. We considered calves radio-tagged in the spring and fall of 2013 and monitored from 2013–2014 as having occurred in the during-treatment era. We considered calves radio-tagged calves in 2016 and 2017 and monitored during 2016–2018 as having occurred in the after-treatment era. During each era, we monitored calf survival and cause of death. We compared survival and cause-specific mortality across the three treatment eras to understand changes in the survival and cause-specific mortality of elk calves prior to, during, and after the mountain lion harvest treatment. Additionally, we evaluated relationships between calf survival and other potentially important covariates, as described below.

Calf capture and sampling

During all three treatment eras, we captured neonate elk calves during an approximately 2-week period near the end of May each year following approved animal care protocols (MSU IACUC#2016-06, UM IACUC# 027-11MHWB-042611). We used ground and helicopter crews to search for female elk that showed signs of having recently given birth. Ground crews attempted to locate neonates by watching for behavioral indications from adult females and/or by searching areas on foot. Each calf was outfitted with an ear-tag radio-transmitter, which was designed to sense periods of inactivity >4 hours and increase the signal pulse rate (mortality mode) if such a period occurred. For each calf we recorded calf sex and several morphometric measurements which were used to obtain an estimate of calf age at capture as well as calf birth mass. To maintain adequate sample sizes for the winter monitoring period, we radio-tagged

additional calves most years between 30 November and 5 January during which calves were either chemically immobilized or net-gunned from a helicopter depending on the terrain.



Figure 4.1 *Hobbled and blindfolded neonatal elk calf with blue ear-tag radio transmitter in right ear.*

Calf monitoring

Using a combination of ground and aerial telemetry, we monitored VHF signals of tagged calves to determine survival status from the day after capture to 30 May of the following year. We monitored each surviving calf every day from its date of capture to 31 August and 2 to 4 times per week thereafter. We used aerial telemetry from fixed-wing aircraft to obtain periodic calf locations. We used calf locations in conjunction with mountain lion and wolf resource selection functions (RSF) to estimate spatial variation in mortality risk (see below).

Investigation of calf mortality

When we detected that the signal from an ear-tag radio that was in mortality mode, which indicated that the calf was dead, we located the calf carcass and performed a mortality investigation. We used characteristics such as consumption pattern, location and presence of claw marks, location and presence of subcutaneous hemorrhaging, width and presence of bite marks, and general characteristics of the kill site to assign causation to each mortality event (Wade and Bowns 2010). We submitted carnivore scat and hair collected during mortality investigations for DNA analysis to determine predator species identity (USFS Rocky Mountain



Figure 4.2 *Cache pile consisting of grass and twigs covering an elk calf carcass.*

Research Center, Missoula, MT). Using inferences from our field mortality investigations and the results of the DNA-based predator identification, we classified each mortality source as mountain lion, wolf, black bear, unknown predator, non-predation, or unknown cause.

Cause-specific mortality and survival analyses

After classifying the cause of each calf mortality, we used cumulative incidence functions (CIFs) to quantify possible changes in calf mortality from each potential cause between the three treatment eras (Heisey and Patterson 2006, Eacker et al. 2016). CIF estimates represented the cumulative probability of mortality from each potential cause over the first year (365 days) of a calf's lifetime. We used Cox-Proportional Hazards models (Cox 1972) to estimate and compare survival rates in the pre-, during-, and post-treatment eras, and to evaluate support for covariates potentially associated with variation in survival for all tagged calves during all years of data collection (2011-14 and 2016-18). We estimated summer and winter survival separately because we expected seasonal differences in risk factors. We used each calf's birthdate as the origin and estimated mortality risk from age 0 to 180 days for summer models, and we used 26 November as the origin and estimated mortality risk for the subsequent 185 days for winter models.

We evaluated a suite of risk factors potentially affecting calf survival. Risk factors included calf sex, birth mass, birth date, population and treatment era, as well as environmental conditions and mountain lion and wolf risk within the individual calve's seasonal range. Treatment era was a three-level factor variable that indicated whether a calf was studied in the pre-, during, or post-treatment era. Environmental conditions included a metric of winter severity and three normalized difference vegetation index (NDVI) metrics representing growing season conditions were estimated for each individual's seasonal range. Risk was estimated from previously published mountain lion and wolf resource selection functions (RSF). For models of summer survival, risk factors included sex, birth mass, birthdate, population (East Fork or West Fork), a Big Hole Valley identifier (a two-level factor describing whether or not a calf was tagged in the Big Hole Valley), treatment era, risk, and NDVI. For models of winter survival,

risk factors included sex, population (East Fork and West Fork), treatment era, risk, and winter severity. Additional details regarding analysis are found in (Eacker et al. 2016, Forzley et al. 2019).

RESULTS

Calf captures, monitoring, and mortality investigations

During the pre-treatment era, we radio-tagged 142 calves in the spring (2011–2012 = 66, 2012–2013 = 76) and 31 calves at the start of winter (2011–2012 = 31, npre-treatment = 173). In the during-treatment era, we radio-tagged 84 calves in the spring of 2013 and also tagged 29 calves in the winter of (2012–2013 = 29, nduring-treatment = 113). During the two post-treatment years, we radio-tagged 183 calves in the spring (2016–2017 = 81, 2017–2018 = 102) and 65 calves at the start of winter (2016–2017 = 40, 2017–2018 = 25, npost-treatment = 248). The total sample size for all three treatment eras was 534 radio-tagged elk calves. We maintained a small sample of calves tagged in the Big Hole Valley throughout the study (n = 16, 13, and 31 in the pre-, during, and post-treatment eras, respectively).

The era-specific sample of calves were relatively balanced by sex (n = 83 females, 90 males; 53 females and 59 males; and 134 females and 113 males in the pre-, during, and post-treatment eras, respectively; 2 calves were of unknown sex). Average estimated birth mass in the pre-, during, and post-treatment eras, respectively was 13.40 kg (SE = 0.20), 14.30 kg (SE = 0.36), and 13.20 (SE = 0.14) for females and 14.90 kg (SE = 0.21), 14.20 kg (SE = 0.30), and 14.50 (SE = 0.13) for male calves. We recorded 19,323 observations in the pre-treatment era (n = 15,708 live, 75 = dead, and 3,540 = not heard), 20,644 observations in the during-treatment era (n = 12,076 live, 35 = dead, and 8,533 = not heard), and 25,185 observations in the post-treatment era (n = 19,419 live, 87 = dead, 5,679 = not heard). We obtained 1,834 estimated calf locations in the pre-treatment era, 919 in the during-treatment era, and 1,514 locations in the post-treatment era.

Cause-specific mortality and cumulative incidence functions

We removed records for 10 of the 534 radio-tagged calves from analyses due to mortality within 24 hours of capture (n = 6), unknown sex (n = 2), or mortality signals detected in inaccessible areas (n = 2). Like many other studies of neonate survival (Griffin et al. 2011), we right censored (i.e., censored after the last observation) 169 radio-tagged calves due to tag loss. We also right censored data for 23 calves that either left the study area or suffered tag failure such that their survival could not be monitored. We estimated cause-specific mortality using data from 197 mortalities, 75 in the pre-treatment era, 35 in the during-treatment era, and 87 in the post-treatment era (Table 4.1). Of 534 elk calves, 158 calves were known to have survived to 1 year of age.

Table 4.1 Number of calves that died from black bear predation, mountain lion predation, wolf predation, non-predation, unknown predator, and unknown cause, by elk population and treatment era during pre-treatment, during-treatment, and post-treatment eras.

Population	Cause of mortality	Pre-	During-	Post-	Total
East Fork	Mountain lion	11	7	13	31
	Non-predation	3	1	9	13

	Black bear	6	1	1	8
	Wolf	3	0	3	6
	Unknown predator	3	3	3	9
	Unknown cause	13	7	28	48
	Other	2	1	0	3
West Fork	Mountain lion	16	6	6	28
	Non-predation	2	1	8	11
	Black bear	3	2	4	9
	Wolf	3	0	3	6
	Unknown predator	5	3	1	9
	Unknown cause	5	3	8	16
	Other	0	0	0	0

Estimated CIFs indicated that mountain lion predation in the East Fork was the highest source of known mortality in the pre-treatment (0.16, 95% CI = 0.09–0.24, Figure 4.3) and during-treatment (0.12, 95% CI = 0.04–0.18) eras. However, in the post-treatment era, cumulative mortality rates for mountain lion predation (0.11, 95% CI = 0.03–0.16) and non-predation (0.10, 95% CI = 0.03–0.16) were similar and higher than all other known causes,

despite non-predation mortality being relatively low in the pre- (0.03, 95% CI = 0.00–0.07) and during-treatment (0.02, 95% CI = -0.01–0.05) eras.

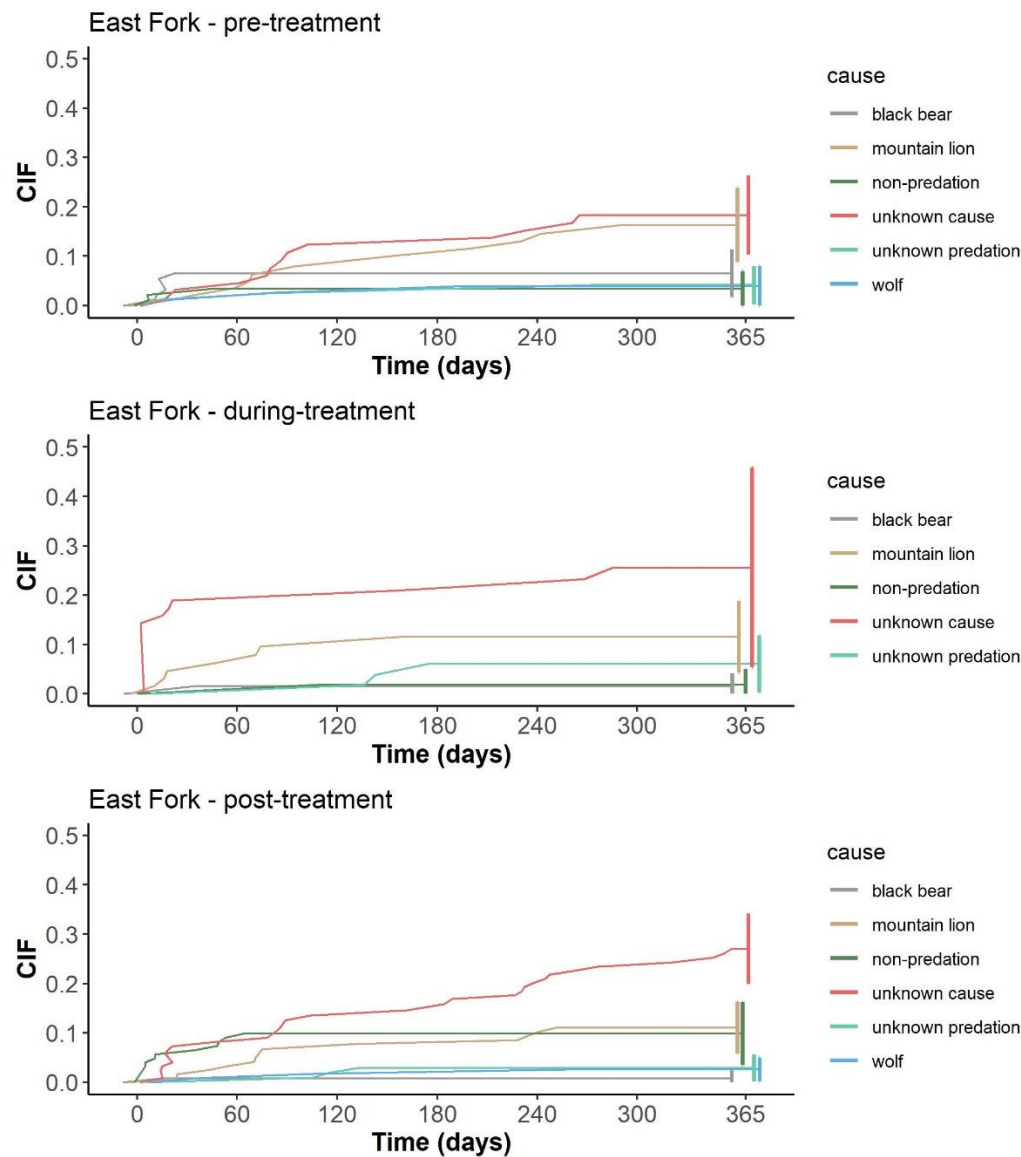


Figure 4.3 Cumulative Incidence Functions (CIF) showing the cumulative probability of calf mortality (y-axis) from 0 to 365 days after birth in the East Fork herd from mountain lions, black bears, wolves, non-predation, unknown causes, and unknown predators in the Bitterroot study area, during pre-treatment, during-treatment, and post-treatment eras. Vertical bars show 95% confidence intervals for the cumulative probability of mortality from each cause at the end of one year.

In the West Fork, estimated CIFs indicated that mountain lion predation was the largest known cause of mortality in both the pre- (0.35, 95% CI = 0.22–0.48) and during-treatment eras (0.24, 95% CI = 0.09–0.38). However, in the post-treatment era, non-predation was the highest

source of known mortality (0.42, 95% CI = 0.02–0.81; Figure 4.4), and cumulative mortality rates for mountain lion predation were relatively low (0.05, 95% CI = 0.00–0.10).

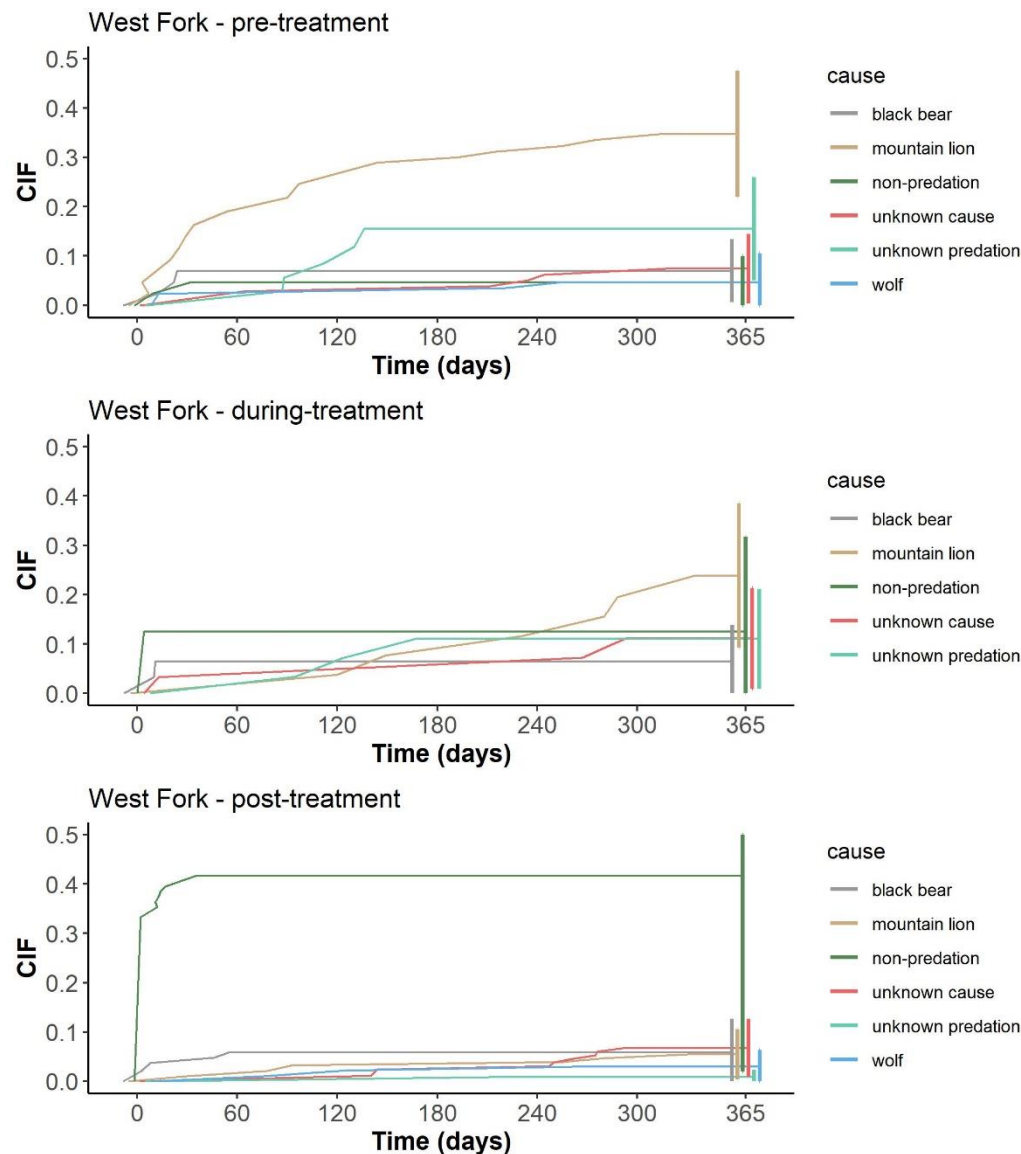


Figure 4.4 Cumulative Incidence Functions (CIF) showing the cumulative probability of calf mortality (y-axis) from 0 to 365 days after birth in the West Fork from mountain lions, black bears, wolves, non-predation, unknown causes, and unknown predators, by treatment era, in the Bitterroot study area during pre-treatment, during-treatment, and post-treatment eras. Vertical bars show 95% confidence intervals for the cumulative probability of mortality from each cause at the end of one year.

Elk calf mortality rate was highest during the first 90 days of the summer season and remained relatively constant across fall and winter. Annual probabilities of black bear and wolf predation were low in all three treatment eras for both populations. Mortality due to black bears and non-predation only occurred during the summer season, whereas mortality from mountain lions, wolves, and unknown causes occurred throughout the year. The cumulative annual

probability of non-predation mortality increased in the post-treatment era in both populations. CIFs related to the annual probability of unknown cause mortality were high for both populations during all three treatment eras (Figure 4.3; Figure 4.4). The cumulative annual probability of unknown cause and unknown predator mortalities were not similar to any single source of known cause mortality and appeared to be a combination of mortality from multiple sources. For example, in some cases, CIFs related to unknown cause and unknown predator mortality were steep during the early summer months (i.e., similar to patterns black bear and non-predation mortality), but also persisted through winter and the following spring (i.e., similar to mountain lion and wolf mortality).

Summer calf survival

Our modeling of summer calf survival yielded considerable model-selection uncertainty with several well-supported models. Due to this model-selection uncertainty, we used model averaging to estimate summer elk calf survival based on all covariates in our final model selection step. Calf sex was our best-supported covariate affecting elk calf survival in summer. Model averaged coefficients indicated that male calves had a higher daily risk of dying than females during summer (HR = 1.68, 95% CI = 1.70–2.37). The daily risk of mortality in the pre- and post-treatment eras was higher for elk calves that occupied areas of higher mountain lion RSF values (HR = 17.25, 95% CI = 1.00–297.32, Figure 4.5). The mean value of the mountain lion RSF covariate for calves that died during the summer during the pre- and post-treatment eras (0.35, 95% CI = 0.33–0.37) was higher than the mean for calves that survived (0.31, 95% CI = 0.30–0.32). Further, that pattern held true regardless of the cause of death: mean values of the summer mountain lion RSF covariate for calves that died due to mountain lions (0.36, 95% CI = 0.34–0.39), wolves (0.37, 95% CI = 0.33–0.41), black bears (0.38, 95% CI = 0.35–0.41), non-predation (0.35, 95% CI = 0.32–0.39), and unknown causes (0.33, 95% CI = 0.29–0.35) were all relatively high and similar compared to values for calves that survived. In contrast to results for the pre- and post-treatment eras, the relationship between summer calf survival and mountain lion RSF was positive in the during-treatment era (Figure 4.5). The mountain lion RSF covariate varied between the East Fork and West Fork elk populations, and the model averaged coefficient

indicated that the strength of the relationship was weaker in the West Fork (0.67, 95% CI = 0.21–2.20).

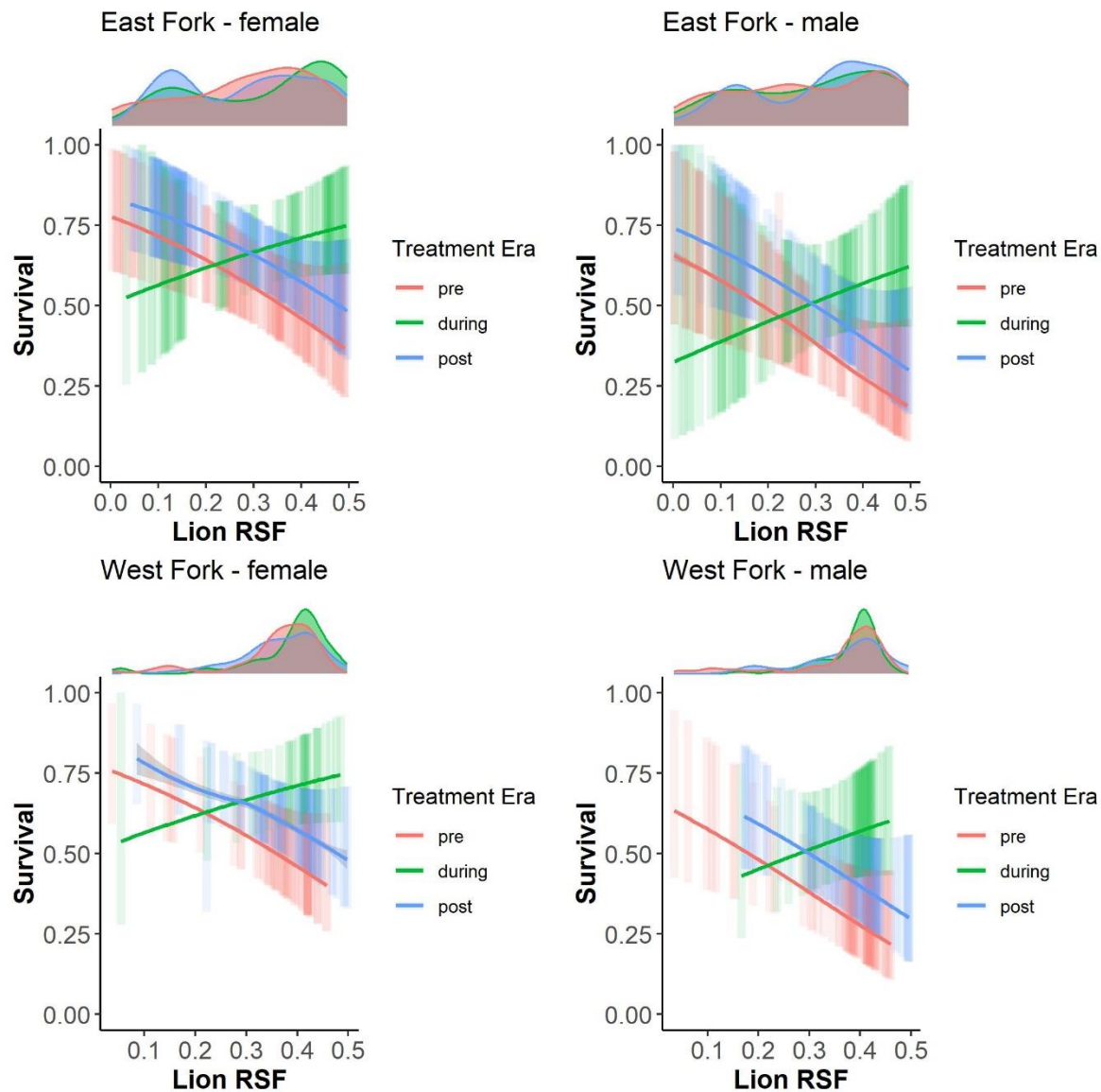


Figure 4.5 Estimated relationship between elk calf summer survival rate and mountain lion RSF values in the area used by a calf in the Bitterroot study area. Data were collected before, during, and after the liberalized carnivore harvest management prescriptions and relationships were estimated using our best-supported summer proportional hazards model. Distributions of observed lion RSF values for calves in each herd and treatment era are provided at the top of each plot.

When estimated using model averaged predictions for the three treatment eras, summer survival rates in the East Fork population were estimated as 0.57 (0.45–0.72), 0.69 (0.56–0.85), and 0.62 (0.52–0.74) for females and 0.39 (0.27–0.57), 0.55 (0.39–0.76), and 0.44 (0.33–0.61) for males, during the pre-, during, and post-treatment eras respectively. Summer survival rates in the West Fork population were estimated as 0.53 (0.39–0.73), 0.72 (0.58–0.90), and 0.70 (0.59–

0.83) for females and 0.35 (0.21–0.57), 0.58 (0.41–0.83) and 0.55 (0.42–0.72) for males, in the pre-, during-, and post-treatment eras respectively. We found that the daily risk of mortality for calves tagged in the Big Hole was lower than that of calves tagged in the East Fork or West Fork (HR = 0.65, 95 % CI = 0.24–1.77). Summer survival rates in the Big Hole sub-unit of the East Fork population were estimated as 0.66 (0.43–0.99), 0.81 (0.64–1.00), and 0.79 (0.62–1.00) for females and 0.50 (0.23–1.00), 0.70 (0.47–1.00) and 0.67 (0.62–0.97) for males, in the pre-, during-, and post-treatment eras respectively.

Winter calf survival

Our best-supported model for winter survival contained three covariates: treatment era, mountain lion RSF, and the interaction between treatment era and mountain lion RSF. In all three treatment eras, model averaged coefficients indicated that calves that occupied areas with higher mountain lion RSF values had a higher daily mortality risk in winter (HR = 8.55, 95% CI = 1.03–71.02, Fig. 4.6). Indeed, the mean value of the mountain lion RSF covariate for calves that died during the winter (0.32, 95% CI = 0.30–0.34) was higher than the mean value for calves that survived (0.28, 95% CI = 0.27–0.28). However, winter mountain lion RSF scores were higher for all calves that died, regardless of the cause of death: mean values of the winter mountain lion RSF covariate for calves that died due to mountain lions (0.35, 95% CI = 0.32–0.38), wolves (0.34, 95% CI = 0.29–0.39), or unknown causes (0.31, 95% CI = 0.28–0.33) were all relatively high and similar. The interaction between the mountain lion RSF covariate and

treatment era indicated that the relationship between winter calf survival and mountain lion RSF covariate was negative in all three treatment eras (Figure 4.6).

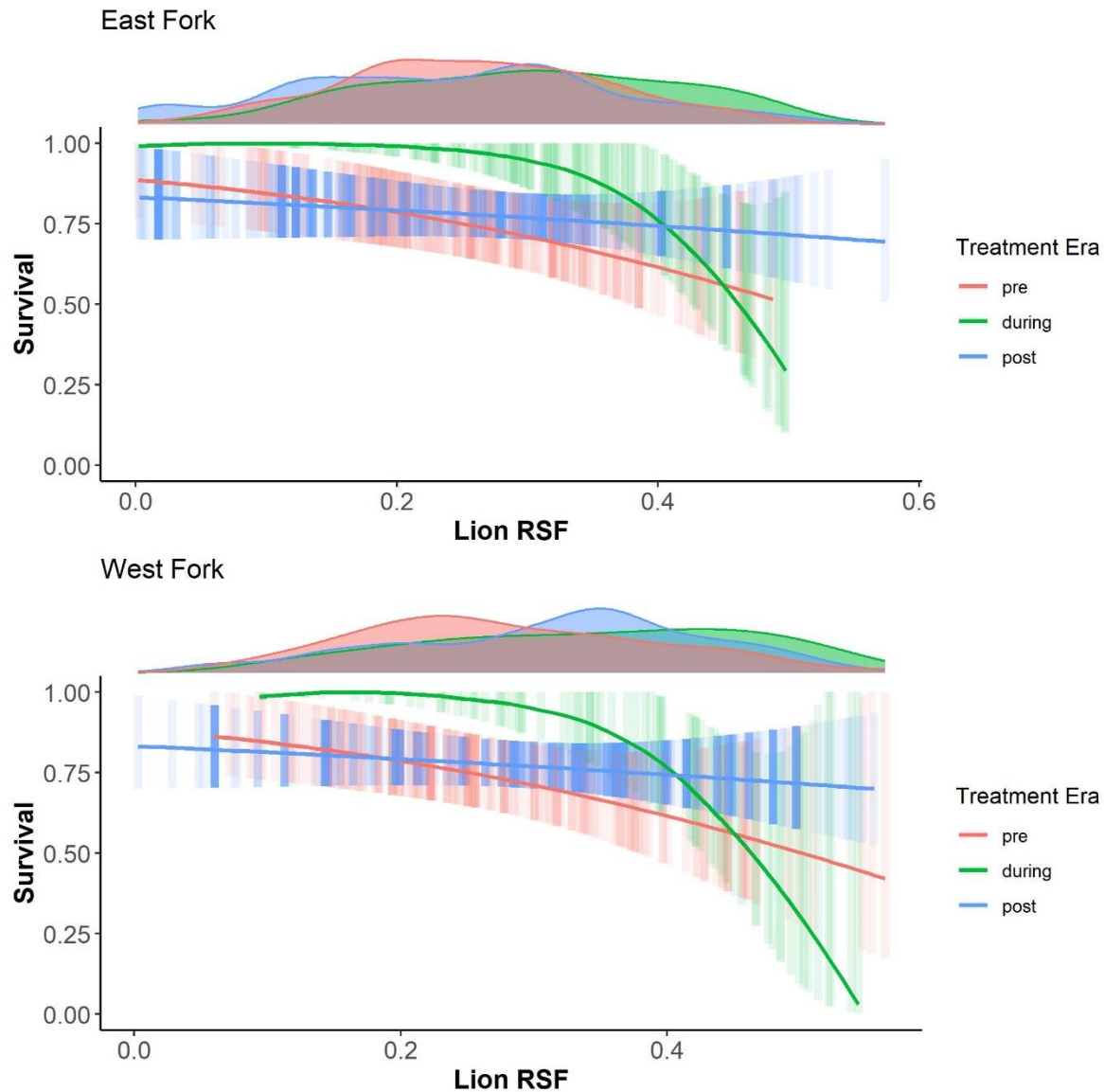


Figure 4.6 *Estimated relationship between elk calf winter survival rate and mountain lion RSF values in the area used by a calf in the Bitterroot study area, Montana, USA. Data were collected before, during, and after the liberalized carnivore harvest management prescriptions in the area, and relationships were estimated using our best-supported winter proportional hazards model. Distributions of observed lion RSF values for calves in each herd and treatment era are provided at the top of each plot.*

Treatment era was included in all but two of our best-supported winter models. Predicted winter survival rates obtained from model-averaging for each treatment era using era- and population-specific values of mountain lion RSF were 0.53 (0.37–0.76), 0.81 (0.72–0.91), and 0.78 (0.70–0.87) for East Fork calves and 0.56 (0.39–0.78), 0.84 (0.75–0.94), and 0.79 (0.71–0.89) for West Fork calves in the pre-, during, and post-treatment eras, respectively.

Annual survival rates

Based on model averaged coefficients from our best-supported summer and winter models, variation in annual survival was related to treatment era, calf sex, and spatial variation in the mountain lion RSF covariate. Annual survival was consistently higher for females than males and similar between populations, and across values of mountain lion RSF that were specific to each population (Table 4.2). At mean values of the mountain lion RSF covariate, point estimates of annual survival rates were lowest in the pre-treatment era, highest in the during-treatment era, and intermediate in the post-treatment era (Table 4.2).

Table 4.2 *East Fork and West Fork herd annual calf survival rates and 95% confidence intervals, for the pre-treatment, during-treatment, and post-treatment eras at mean values of the mountain lion RSF covariate, specific to each sex, herd, and treatment era in the Bitterroot study area.*

Population	Sex	Era	Annual Survival
East Fork	Male	Pre	0.21 (0.05–0.36)
		During	0.44 (0.21–0.68)
		Post	0.34 (0.13–0.56)
East Fork	Female	Pre	0.30 (0.11–0.48)
		During	0.55 (0.30–0.82)
		Post	0.49 (0.24–0.73)
Population	Sex	Era	Annual Survival
West Fork	Male	Pre	0.18 (0.03–0.34)
		During	0.48 (0.24–0.74)
		Post	0.43 (0.20–0.67)
West Fork	Female	Pre	0.29 (0.10–0.47)
		During	0.59 (0.32–0.85)
		Post	0.55 (0.30–0.81)

DISCUSSION

Our analysis of annual elk calf survival offers an opportunity to understand the effects of mountain lion harvest management regulations on elk calf survival, while controlling for potential confounding variables. Our estimates of elk calf survival provide evidence that the mountain lion harvest treatment did coincide with increased summer, winter, and annual elk calf survival during the mountain lion harvest treatment, and estimated rates of annual elk calf survival in the during-treatment era nearly doubled during 1–2 years of increased mountain lion harvest. However, our results also suggest that the initial increases in annual survival in the during-treatment era were reduced to intermediate levels 4-years after treatment and were only about 10 percent higher than pre-treatment-era levels. These findings echo results of previous studies that link carnivore harvest treatments to increased rates of elk calf survival (White et al. 2010) and results of other studies that demonstrated a quick return to pre-predator-control conditions (Council 1997, Hayes et al. 2003).

Although overlapping confidence intervals between the survival rates associated with the calves in each of the three treatment eras weakens our inference, the inclusion of the treatment-era covariate was well supported by model selection, and several well-supported summer and winter calf survival models included the effects of a short-lived treatment-era response. Therefore, our modeling of elk calf survival data suggests that the mountain lion harvest treatment did coincide with short-term increases in elk calf survival rate. However, our goal was to understand whether any potential changes to calf survival were related to changes in the probabilities of mountain lion predation before, during, and after the harvest treatment. We cannot confidently conclude that the short-term increases in elk calf survival were caused by decreased rates of mountain lion predation because of the high numbers of calves that died from unknown causes.

Our inferences as to changes in elk calf survival and mortality sources are limited by potential confounding between changes in mountain lion harvest and changes in black bear and wolf harvest. The mountain lion harvest treatment overlapped entirely with extended black bear hunting seasons and increased individual hunter annual harvest limits for wolves. However, data suggests that liberalized black bear and wolf harvest regulations did not result in change in the realized harvest for either species, and there was no evidence to indicate decreases in the abundance of either species. Perhaps the number of black bears and wolves harvest annually was not sufficient to exert change on populations of either species in the area, and indeed, limiting harvest to public hunting and trapping has been showed to be insufficient to limit carnivore populations in other areas (Ballard and Miller 1990, Robichaud and Boyce 2010). Unlike liberalized black bear and wolf harvest regulations, the mountain lion harvest treatment was largely successful, and quotas were 95 and 85 percent achieved, for males and females respectively.

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